

## NEW GENUS OF FOSSIL FAGACEAE FROM THE SANTONIAN (LATE CRETACEOUS) OF CENTRAL GEORGIA, U.S.A.

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A new genus and species (*Antiquacupula sulcata*) is established for fossil staminate flowers, bisexual flowers, fruits, and cupules from the late Santonian (Late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, U.S.A. Together with *Protofagaceae*, recently described from the same locality, these remains constitute the earliest fossil evidence of the Fagaceae *sensu lato*. Staminate flowers of the new genus are pedicellate, with six free tepals in two cycles of three, 12 free stamens, and a vestigial gynoecium with three styles. Bisexual flowers are epigynous and actinomorphic, with six free tepals in two whorls, 12 free stamens, and a syncarpous gynoecium with three styles. The ovary is trilobular, with two anatropous, apically pendulous ovules per locule. The styles are partially connate below, with trichomes around and between the style bases. Fruits are triangular in cross section, with nearly equal sides, and contain a single seed. Cupules comprising multiple series of bracts contain at least six fruits. The staminate and bisexual flowers both have slender, thin-walled nectary lobes between the filament bases and distinctive, multicellular glandular structures on the surface of the gynoecium. Pollen grains found in the anthers and on the surface of the flowers and fruits are small and tricolporate, with a finely perforate tectum. Comparison of these fossils to extant and fossil taxa clearly indicates a relationship to extant Fagaceae *sensu lato*, based on the presence of the cupule and flower and fruit morphology. The discovery of *Antiquacupula*, in addition to *Protofagaceae*, indicates an early divergence of at least two lineages within the Fagaceae, both with cupules, by the Santonian. In addition, *Antiquacupula* shares several characters with extant rosids and hamamelids and may be a key taxon for clarifying the relationships among these groups as well as within the Fagaceae.

### Introduction

The family Fagaceae *sensu lato* comprises nine genera and nearly a thousand extant species of monoecious trees and shrubs, including the beeches, oaks, and chestnuts (Heywood 1993; Linder and Crisp 1995). The group is predominantly distributed in the Northern Hemisphere, except for several genera that extend into the Southern Hemisphere, and *Nothofagus*, which is restricted to the Southern Hemisphere (Heywood 1993). The earliest evidence of Fagaceae *sensu lato* in the fossil record is documented by dispersed pollen similar to that produced by extant *Nothofagus* from the early Campanian and younger strata of southern Gondwana (Dettmann et al. 1990) and *Protofagaceae* flowers and associated fruits and cupules from the late Santonian (previously thought to be early Campanian; see note added in proof) of southeastern North America (Herendeen et al. 1995). Early evidence of Fagaceae *sensu stricto* (i.e., excluding *Nothofagus*, which is now treated as a distinct family, the Nothofagaceae), is based on dispersed castaneoid pollen reported by Chmura (1973) from the Maastrichtian of California, but the affinities of these grains have been questioned because of the difficulty in distinguishing castaneoid pollen from that of other rosids (Crepet 1989; Crepet and Nixon 1989a). Megafossils assigned to the Fagaceae *sensu stricto* have been recovered from the early and middle Eocene of Tennes-

see (Crepet and Daghlian 1980; Jones and Dilcher 1988; Crepet and Nixon 1989a), the Eocene of Oregon (Manchester 1981, 1994), the Oligocene of Texas (Daghlian and Crepet 1983; Crepet and Nixon 1989b), and several other localities of early Tertiary age (see Herendeen et al. [1995] for a review).

The Fagaceae *sensu lato* are characterized by the presence of a cupule and have been divided traditionally among two or three subfamilies, the Fagoideae, Castaneoideae, and Quercoideae (Forman 1964, 1966a; Hutchinson 1967; Abbe 1974; Jones 1986; Heywood 1993). Recent cladistic analyses have shown the Fagaceae *sensu lato* to be paraphyletic, and they support recognition of the genus *Nothofagus* as a distinct family (the Nothofagaceae) separate from the Fagaceae *sensu stricto*. Analyses of morphological data by Nixon (1989) placed the Fagaceae *sensu stricto* in a basal position, with the Nothofagaceae resolved as sister group to the “higher” hamamelids (e.g., Betulaceae, Juglandaceae, Myricaceae). Recent cladistic analyses based on chloroplast DNA data also resolve the Fagaceae *sensu lato* as paraphyletic but support Nothofagaceae as basal, with Fagaceae *sensu stricto* resolved as sister group to the “higher” hamamelids (Chase et al. 1993; Manos et al. 1993; Martin and Dowd 1993; Manos and Steele 1997).

The structure and origin of the fagaceous cupule have been interpreted variously as fused inflorescence bracts, a *de novo* intercalary structure of the inflorescence axis, or a cladode-like structure formed from the outer (ultimate order) sterile axes of the dichasial inflorescence (Berridge 1914; Hjelmqvist 1948; Brett 1964; Forman 1966b; Abbe 1974; Endress 1977; MacDonald 1979; Fey 1981; Fey and Endress 1983; Kaul

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and Abbe 1984; Nixon 1989; Jenkins 1993; Herendeen et al. 1995). Whatever its morphological origin, given the paraphyly of the Fagaceae *sensu lato*, it is equally parsimonious to hypothesize independent origins of the cupule in *Nothofagus* and Fagaceae *sensu stricto* as it is to interpret the cupules as homologous structures that were lost in the “higher” hamamelids (Nixon 1989; Manos et al. 1993; Herendeen et al. 1995; Manos and Steele 1997). Evidence from the paleobotanical record of early, extinct members of the group may help to clarify relationships within the family and also to illuminate the evolutionary history of the cupule.

The recent description of *Protofagacea allonensis*, a genus of fossil Fagaceae *sensu lato* from the Santonian of North America, by Herendeen et al. (1995) significantly extended the macrofossil record of the group. Staminate flowers and associated fruits and cupules of *Protofagacea* indicate a relationship to extant Fagaceae *sensu lato*, but the genus also shares some characters with Nothofagaceae. In this article we describe a new genus from the same locality as *Protofagacea*. The new fossil flowers, fruits, and cupules also exhibit features of the Fagaceae *sensu lato* but are morphologically distinct from *P. allonensis*. This material establishes the divergence of at least two lineages within Fagaceae *sensu lato* by the late Santonian.

### Material and Methods

The fossil material described here was collected from the south pit (Allon quarry) of the Atlanta Sand and Supply Company (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W) in Gaillard, Georgia, ca. 9.5 km southeast of Roberta in Crawford County. The material was isolated from a carbonaceous clay lens that was exposed on the south face of the Allon quarry. The clay lens has been assigned to the Buffalo Creek Member of the Gaillard Formation (Huddleston and Hetrick 1991). Palynological analyses indicate that the Gaillard Formation is of late Santonian age (Christopher 1979 and personal communication 1998 [see note added in proof after Literature Cited]; Huddleston and Hetrick 1991). The Allon fossil flora contains a diverse assemblage of angiosperms, gymnosperms, ferns, and bryophytes, preserved as fusainized and lignitic mesofossils (Herendeen et al. 1995; Crane and Herendeen 1996; Keller et al. 1996; Magallón-Puebla et al. 1996; Konopka et al. 1997 and in press).

The material was prepared by dissolving bulk samples of clay in water and then washing through a series of sieves (finest mesh 125 µm). Isolated plant material was cleaned with HCl, followed by HF, and then thoroughly washed in water. The fossil material was air-dried and examined using

a binocular stereomicroscope. Specimens were mounted on stubs, coated with gold, and examined with an Amray 1810 scanning electron microscope. After initial scanning, selected specimens were partially dissected to reveal internal anatomy and then recoated and scanned. All fossil specimens are deposited in the paleobotanical collections of the Department of Geology, Field Museum, Chicago (PP).

### Systematics

Family—Fagaceae *sensu lato*

Genus—*Antiquacupula* Sims, Herendeen, and Crane, gen. nov.

Type Species—*Antiquacupula sulcata* Sims, Herendeen, and Crane, sp. nov.

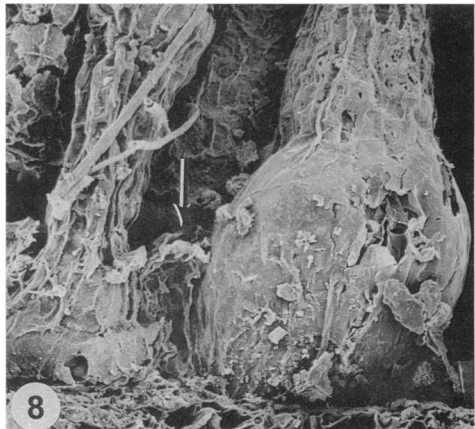
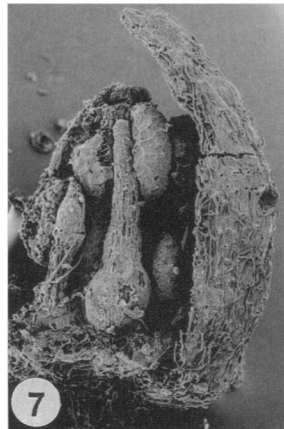
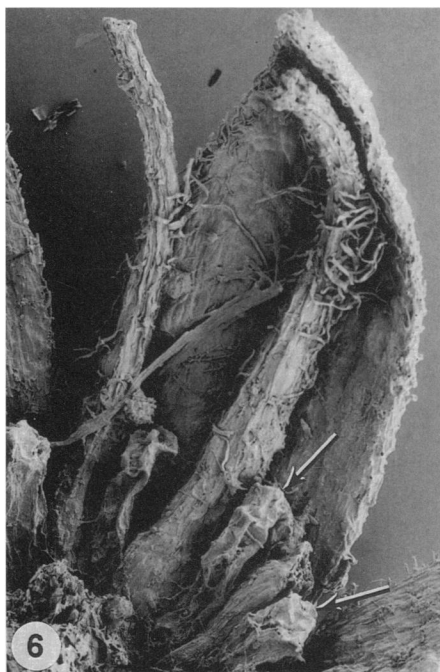
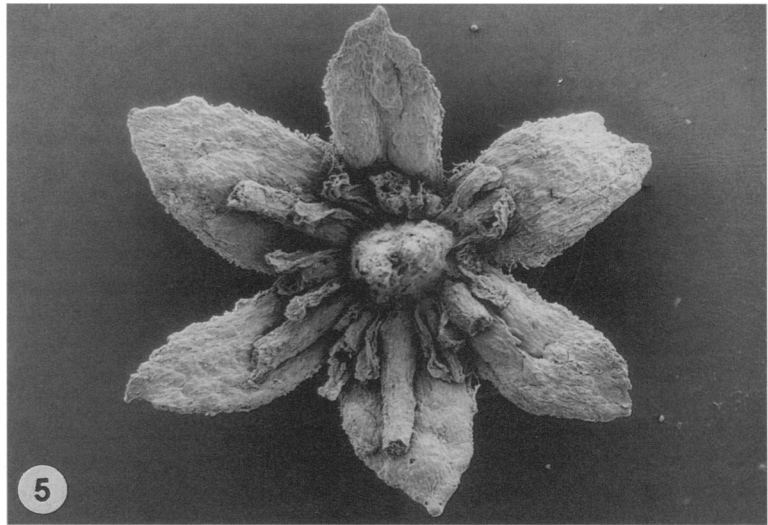
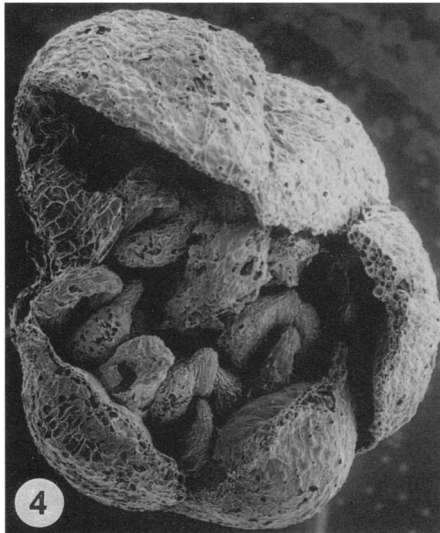
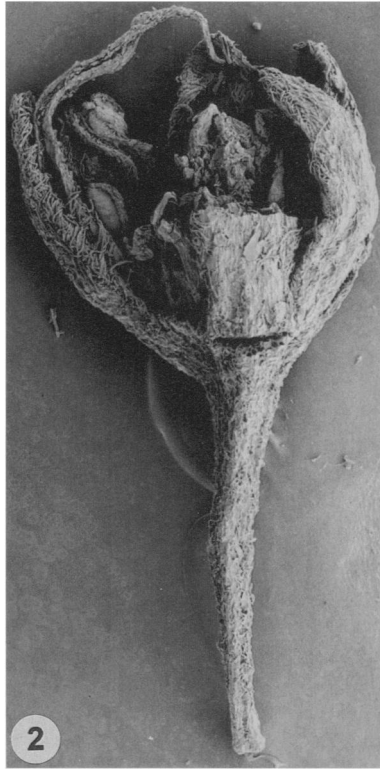
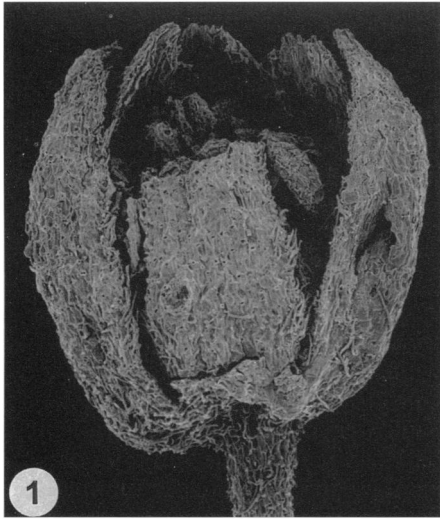
### Generic Diagnosis

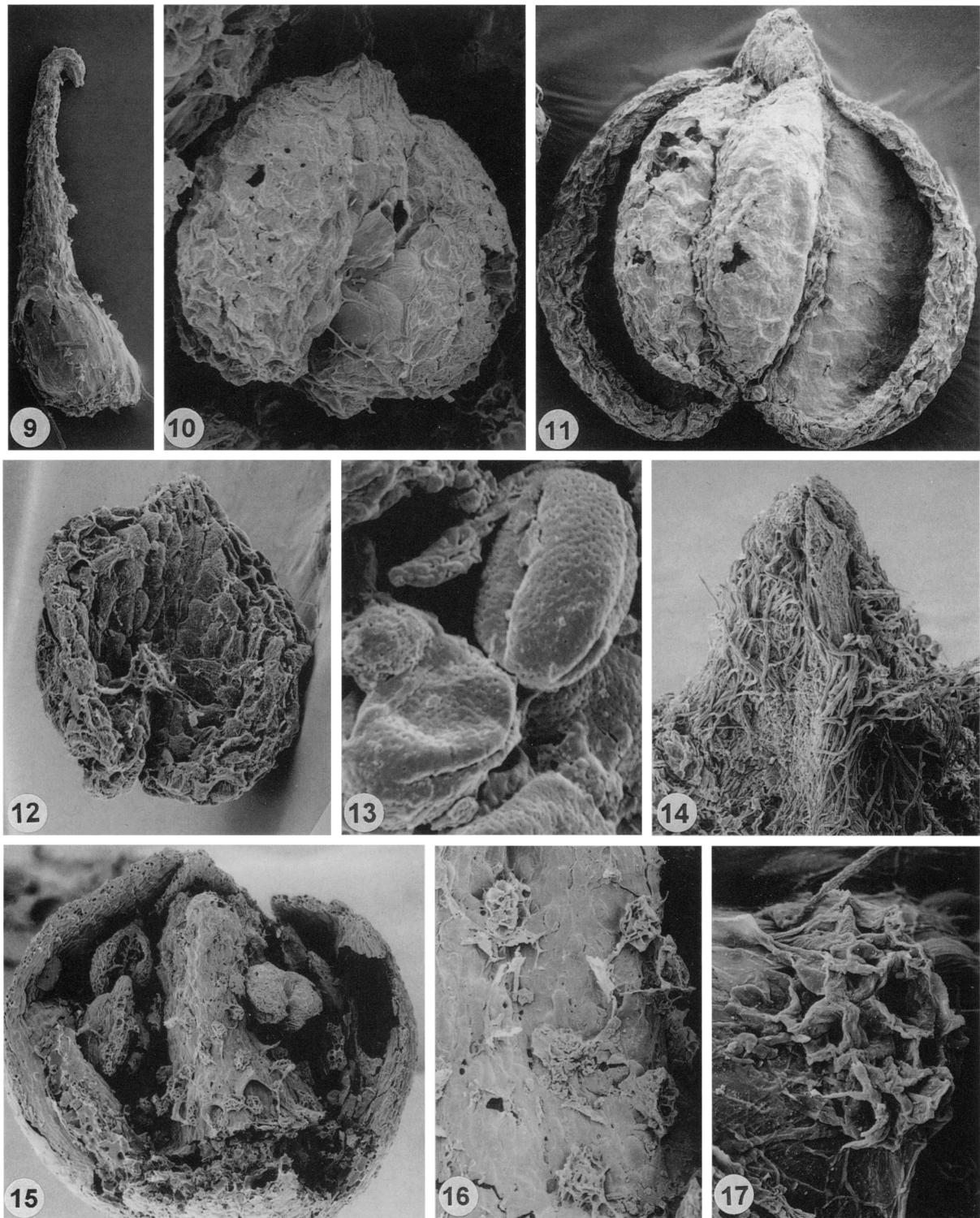
Staminate flowers pedicellate, actinomorphic; tepals free, imbricate, in two cycles of three; stamens free in two cycles of six; stamen cycle opposite tepals develops first, followed by cycle alternate to tepals; anthers dorsifixed with longitudinal dehiscence slits; pollen grains small, tricolporate, tectum finely perforate; slender, thin-walled structures (interpreted as nectary lobes) alternate with stamens; vestigial gynoeceum with three short style lobes, ovary absent; numerous small, multicellular, glandular structures scattered on the surface of style bases; gynoeceum and stamen filaments surrounded by simple trichomes.

Bisexual flowers epigynous, actinomorphic; tepals free, imbricate, in two cycles of three; stamens free, in two cycles of six; anthers dorsifixed with longitudinal dehiscence slits; pollen grains small, tricolporate, tectum finely perforate; slender, thin-walled structures located between each filament base (interpreted as nectary lobes); gynoeceum tricarpellate, ovary inferior, trilobular, placentation apical, ovules anatropous, two per locule; styles three, partially connate at the base; surface of ovary covered with simple trichomes; numerous small, multicellular glandular structures scattered on the surface of style bases.

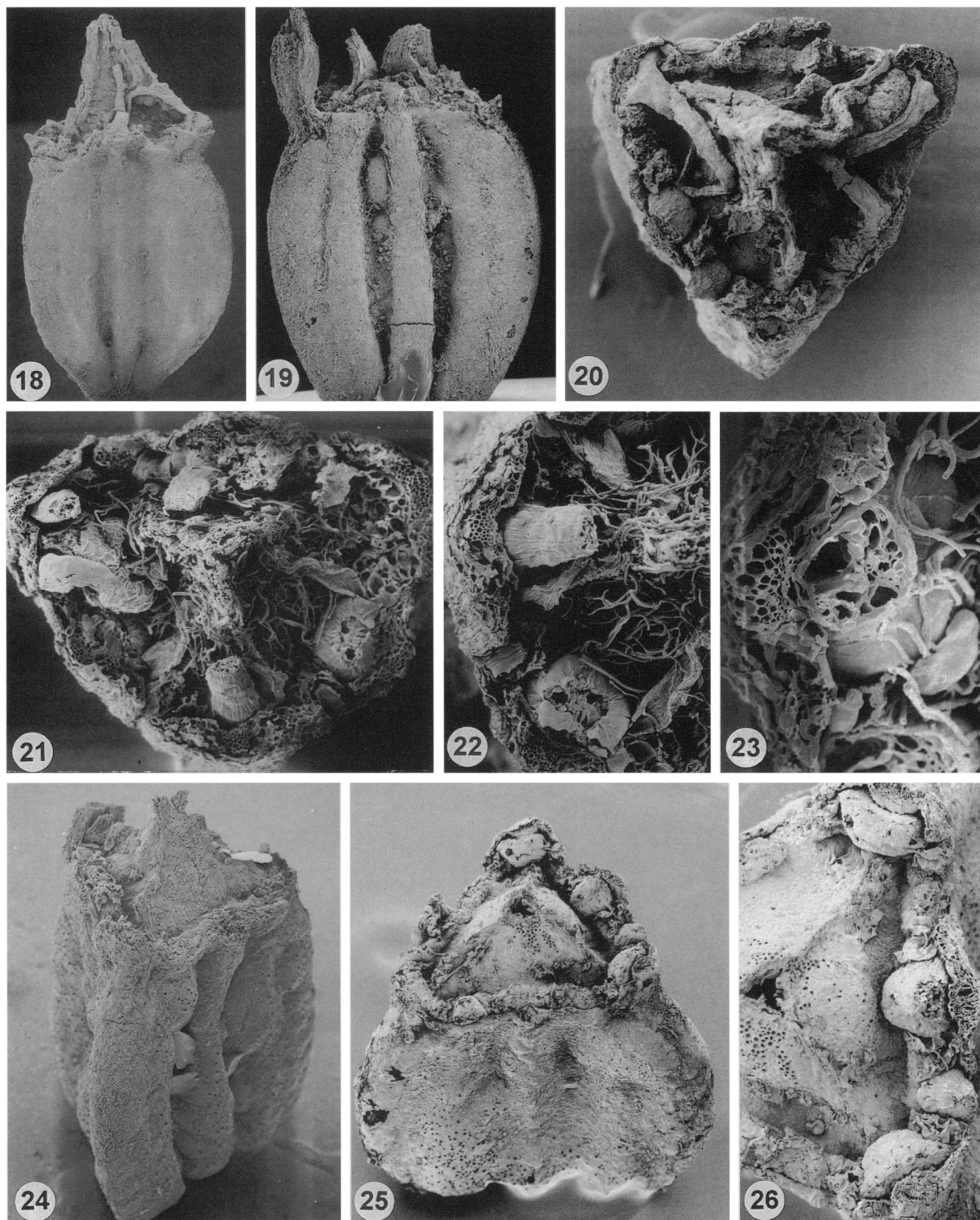
Cupules comprise multiple series of bracts and contain at least six closely aggregated bisexual flowers/fruits. Fruits triangular in cross section with sides of approximately equal length; outer tepals located on the corners of the fruits, inner tepals centered on each face; associated pollen grains small, tricolporate, tectum finely perforate; slender, thin-walled structures (interpreted as nectary lobes) located between filament

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**Figs. 1–8** Staminate flowers of *Antiquacupula sulcata*. Fig. 1, Lateral view of staminate flower bud with tips of stamens visible; PP44771; × 70. Fig. 2, Lateral view of mature staminate flower with pedicel and attached anthers; PP44767; × 40. Fig. 3, Tepal, showing acute apex and trichomes on margins; PP44771; × 135. Fig. 4, Staminate flower, showing anthers and styles; PP44768; × 75. Fig. 5, Staminate flower, showing six tepals in two cycles, 12 filaments opposite and alternate to the tepals, elongated nectary lobes between stamen bases, and gynoeceum of three fused style bases; PP44769; × 30. Fig. 6, Detail of staminate flower, showing filaments with trichomes, swollen filament bases, and elongated nectaries between the stamens. Arrows indicate two of the nectaries. PP44770; × 60. Figs. 7, 8, Partially dissected bud of staminate flower; PP44771. Fig. 7, Lateral view of partially dissected bud, showing stamens of two different cycles; the cycle opposite the tepals has anthers placed higher and more enlarged filament bases; × 70. Fig. 8, Detail of stamen bases, showing difference in swelling of the filament bases between the two cycles of stamens and an elongated nectary (arrow) between the filament bases; × 280.

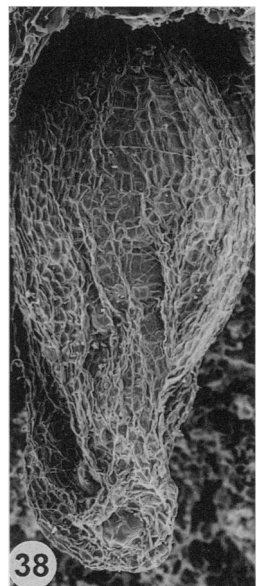
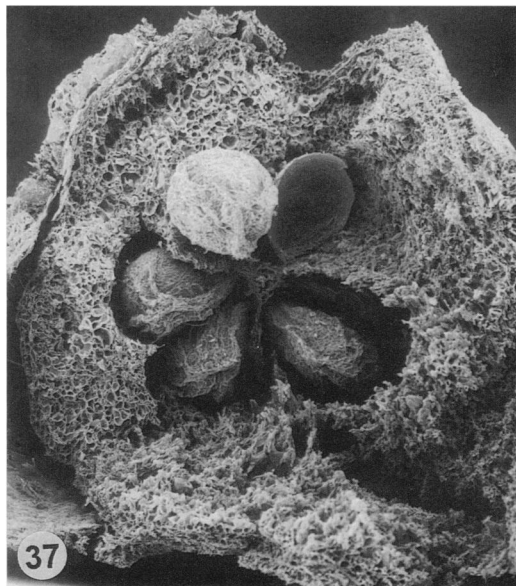
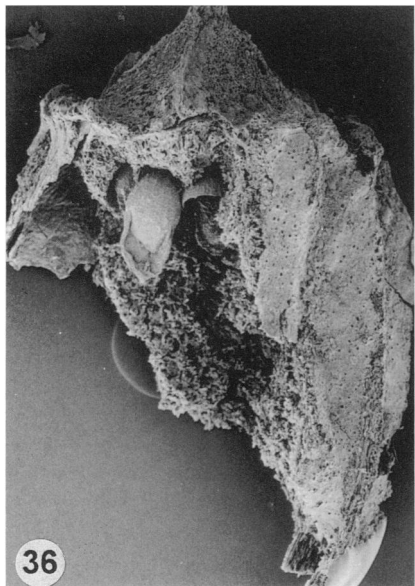
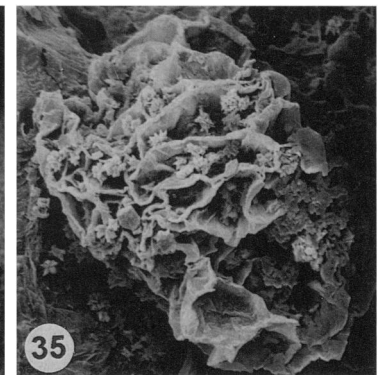
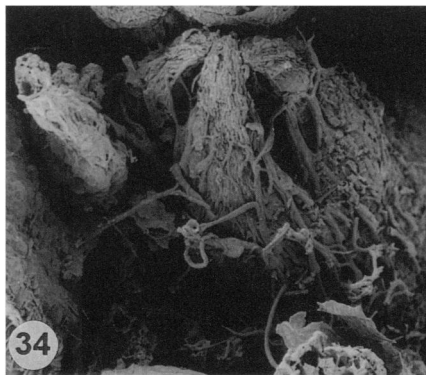
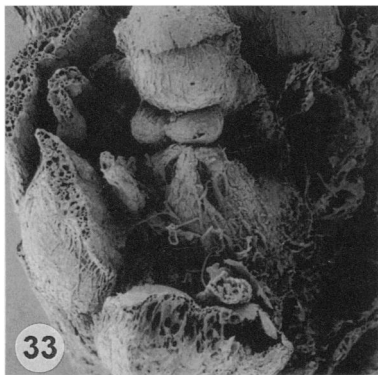
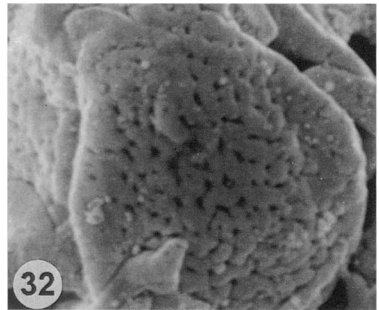
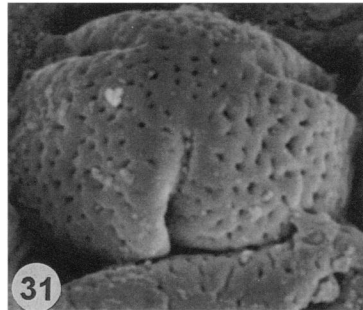
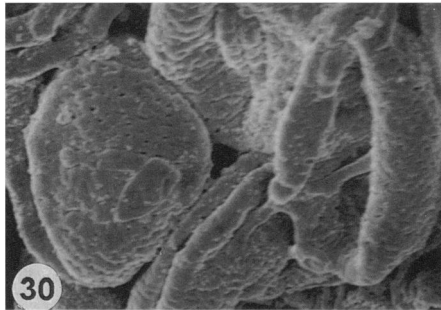
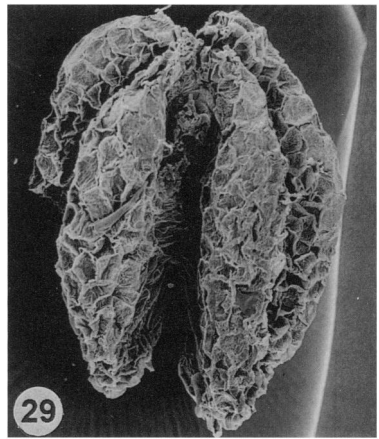
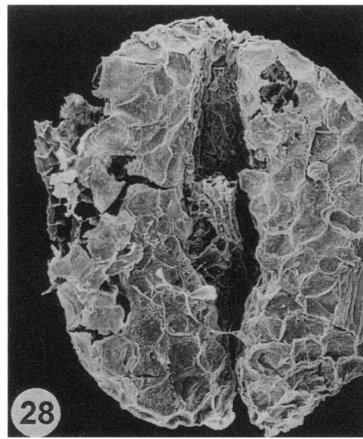
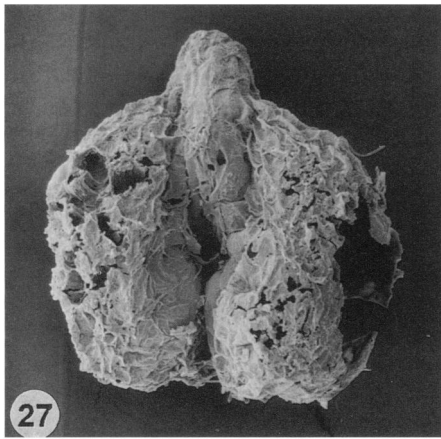


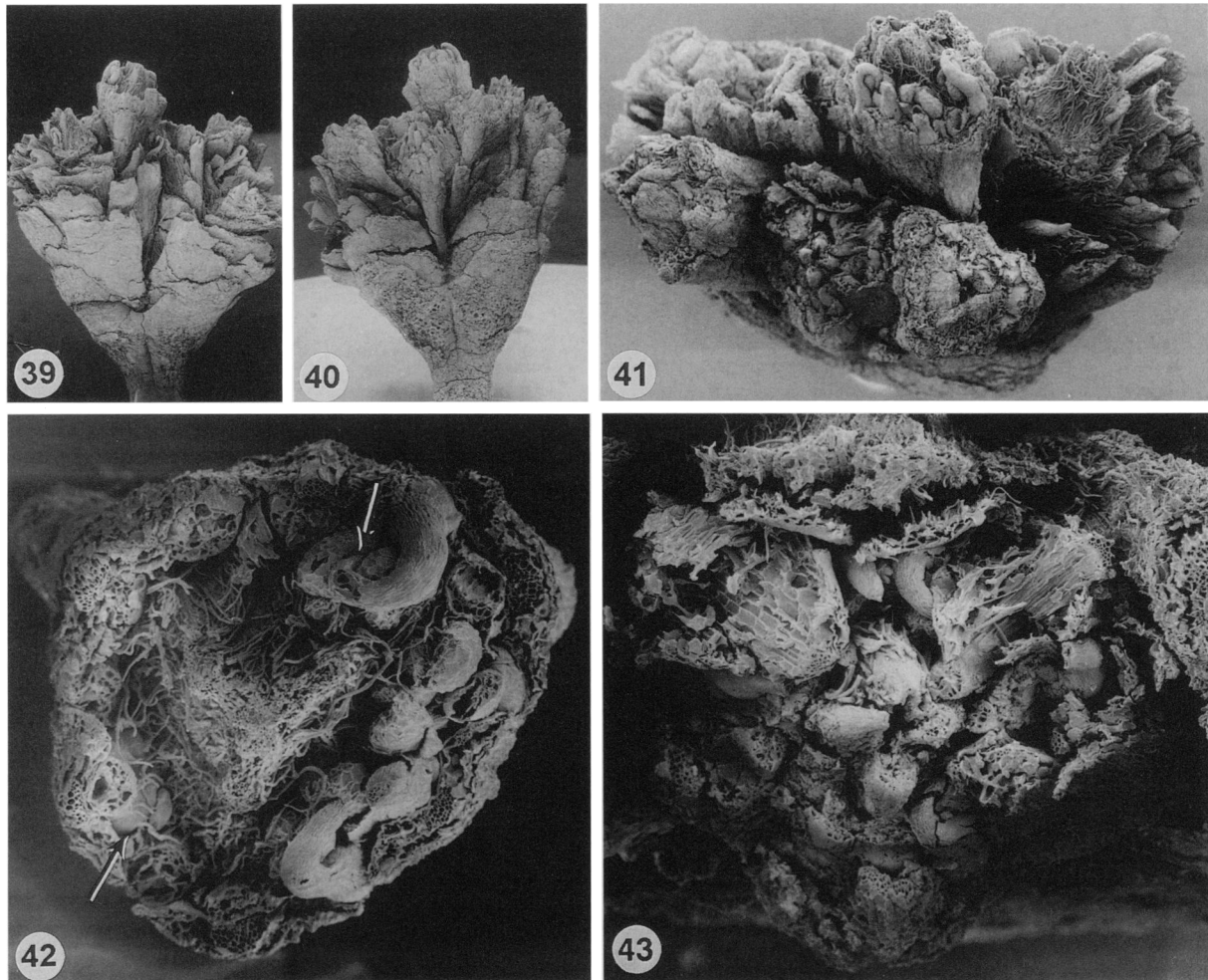


**Figs. 9–17** Staminate flowers of *Antiquacupula sulcata*. Fig. 9, Filament from staminate flower, showing enlarged filament base and apical hook to dorsifixed anther; PP44771;  $\times 150$ . Fig. 10, Ventral side of anther from staminate flower, with apical projection; PP44768;  $\times 350$ . Fig. 11, Mature anther (isolated) with open pollen sacs, showing smooth inner surface of thecae and apical projection; PP44756;  $\times 250$ . Fig. 12, Dorsal side of immature anther from staminate flower bud, showing point of attachment of filament and partial separation of thecae; PP44771;  $\times 350$ . Fig. 13, Pollen of *A. sulcata* from staminate flower; tricolporate grains with finely perforate tectum; PP44767;  $\times 2800$ . Fig. 14, Enlargement of dissected staminate flower, showing three styles, fused at the base, and trichomes around and between the base of the styles; PP44793;  $\times 87$ . Fig. 15, Partially dissected staminate flower bud, showing gynoecium and two cycles of anthers; PP44768;  $\times 75$ . Fig. 16, Detail of gynoecium surface, showing multiple small glands scattered on the surface; PP44768;  $\times 200$ . Fig. 17, Detail of gland on surface of gynoecium; PP44769;  $\times 800$ .



**Figs. 18–26** Fruits of *Antiquacupula sulcata*. Fig. 18, Lateral view of fruit showing fused styler base and moderate ribbing of fruit wall; PP44761;  $\times 15$ . Fig. 19, Lateral view of fruit with attached tepal and well-developed ribbing of fruit wall; PP44760;  $\times 15$ . Fig. 20, Apical view of mature fruit showing attached filaments and styles united at the base; PP44761;  $\times 30$ . Figs. 21, 22, Immature fruit; PP44765. Fig. 21, Apical view of fruit with trichomes, stamens with attached anthers, swollen filament bases, and nectary lobes between filament bases;  $\times 75$ . Fig. 22, Detail showing trichomes, broken tepal base, swollen filament bases and nectary lobes;  $\times 100$ . Fig. 23, Detail of swollen filament base from fruit preserved in cupule; PP44751, holotype;  $\times 225$ . Fig. 24, Oblique view of abraded, mature fruit; PP44757;  $\times 25$ . Fig. 25, Oblique view of abraded, mature fruit, showing partially preserved style bases and nectary lobes; PP44594;  $\times 20$ . Fig. 26, Detail of apex of an abraded fruit, showing characteristic preservation of tepals, swollen stamen bases, nectary lobes, and styles; PP44594;  $\times 37$ .





**Figs. 39–43** Immature cupule of *Antiquacupula sulcata*; PP44751, holotype. Figs. 39, 40, Lateral view from both sides showing four primary lobes and bracts of the cupule;  $\times 10$ . Fig. 41, Slightly oblique apical view showing five fruits *in situ*;  $\times 25$ . Fig. 42, Tricarpellate fruit from cupule. Note attached anthers and swollen filament bases.  $\times 40$ . Fig. 43, Detail of tetracarpellate fruit from cupule;  $\times 85$ .

bases; numerous small, multicellular glandular structures dispersed on the surface of style bases; mature fruits contain a single seed.

**Species**—*Antiquacupula sulcata* Sims, Herendeen, and Crane, sp. nov. (Figs. 1–50)

#### *Specific Diagnosis*

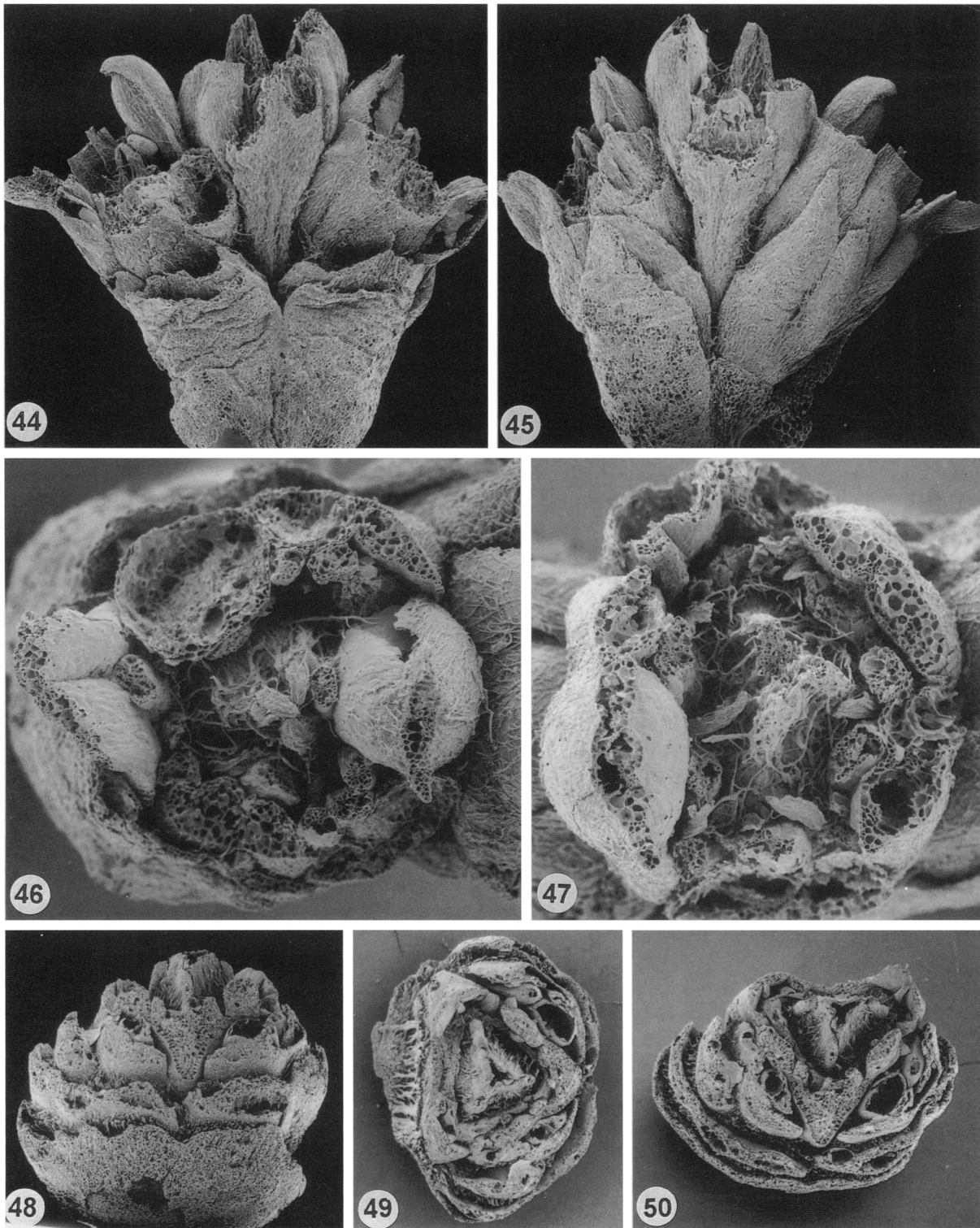
**Staminate flower.** As for the genus, with the following additions: staminate flowers ca. 2–3 mm in diameter; tepals ca. 1 mm long, ca. 0.25 mm wide at the

base, tapering to an acute apex; simple trichomes on margins, tip, and exterior surface of tepals; anthers ca. 0.1–0.3 mm long with distinctive knoblike apical projection; filaments with swollen bases at maturity; pollen grains small (polar axis ca. 12–13  $\mu\text{m}$  long, diameter ca. 8–11  $\mu\text{m}$ ); slender nectary lobes located between each filament base, ca. 0.1 mm in diameter, ca. 0.4 mm long; multicellular glandular structures on surface of style bases, ca. 0.4–0.6 mm in diameter.

**Bisexual flower.** As for the genus, with the follow-

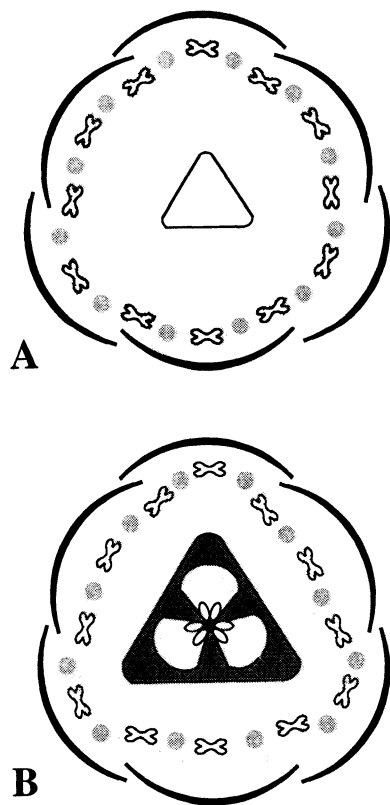
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**Figs. 27–38** Androecium and gynoecium of bisexual flowers of *Antiquacupula sulcata*. Fig. 27, Ventral view of anther from fruit, with apical projection; PP44753;  $\times 250$ . Fig. 28, Dorsal view of anther from fruit, showing attachment point of filament; PP44765;  $\times 175$ . Fig. 29, Anther from fruit preserved in cupule; PP44751, holotype;  $\times 175$ . Figs. 30–32, Pollen of *A. sulcata* from isolated fruits. Fig. 30, Pollen showing finely perforate tectum of tricolporate grains; PP44761;  $\times 2800$ . Figs. 31, 32, Detail of pollen showing exine structure at poles (fig. 31, PP44761;  $\times 5000$ ) and equator (fig. 32, PP44761;  $\times 5000$ ). Fig. 33, Bisexual flower from cupule (lateral fruit from cupule in figs. 39–41) with styles; PP44753;  $\times 50$ . Fig. 34, Detail of specimen in fig. 33, showing basal united portion of styles and trichomes around and between style bases;  $\times 120$ . Fig. 35, Detail of multicellular gland on surface of gynoecium; PP44761;  $\times 800$ . Figs. 36–38, Fruit structure; PP44762. Fig. 36, Lateral view of partially dissected fruit, showing apically attached ovules;  $\times 25$ . Fig. 37, View into apex of dissected fruit, showing three locules with two ovules per locule and spongy mesocarp between locules and fruit wall;  $\times 50$ . Fig. 38, Detail of anatropous ovule;  $\times 120$ .



**Figs. 44–50** Cupules of *Antiquacupula sulcata*. Figs. 44–47, Immature cupule with three fruits; PP44753. Figs. 44, 45, Lateral view from both sides, illustrating four primary lobes and arrangement of bracts;  $\times 30$ . Fig. 46, Apical view of lateral fruit. Fig. 47, Apical view of central fruit;  $\times 75$ . Figs. 48–50, Partial cupule with one mature fruit; PP44752; all  $\times 25$ . Fig. 48, Lateral view of cupule illustrating bract structure. Fig. 49, Apical view showing triangular fruit outline (cf. figs. 20, 24, 25). Fig. 50, Oblique view of cupule, illustrating bract structure.





**Fig. 51** Schematic diagrams of fossil staminate flower (A) and bisexual flower (B) summarizing the structural organization of *Antiquacupula sulcata*.

ing additions: simple trichomes on margins, tip, and abaxial surface of tepals; anthers ca. 0.1–0.3 mm long with distinctive knoblike apical projection; pollen grains small (polar axis ca. 12–13  $\mu\text{m}$  long, diameter ca. 8–11  $\mu\text{m}$ ); filament bases swollen at maturity; slender nectary lobes located between each filament base, ca. 0.1 mm in diameter, ca. 0.4 mm long; multicellular glandular structures on surface of style bases, ca. 0.4–0.7 mm in diameter.

**Fruit.** As for the genus, with the following additions: fruits ca. 2–4 mm in length, ca. 2–3 mm in maximum width; longitudinally ribbed fruit walls, with three to five ribs per side; filaments have swollen bases at maturity; slender nectary lobes located between each filament base, ca. 0.1 mm in diameter and ca. 0.4 mm long; multicellular glandular structures on surface of style bases, ca. 0.4–0.7 mm in diameter.

#### *Holotype*

PP44751 (figs. 23, 29, 39–43).

#### *Additional Material (Paratypes)*

**Staminate flowers.** PP44766, PP44767 (figs. 2, 13), PP44768 (figs. 4, 10, 15, 16), PP44769 (figs. 5, 17), PP44770 (fig. 6), PP44771 (figs. 1, 3, 7–9, 12), PP44793 (fig. 14).

**Cupules.** PP44752 (figs. 48–50), PP44753 (figs. 27, 33, 34, 44–47).

**Isolated fruits.** PP44594 (figs. 25, 26), PP44757 (fig. 24), PP44758, PP44759, PP44760 (fig. 19), PP44761 (figs. 18, 20, 30–32, 35), PP44762 (figs. 36–38), PP44763, PP44764, PP44765 (figs. 21, 22, 28), PP44766, PP44821, PP44822.

**Isolated anthers.** PP44755, PP44756 (fig. 11).

#### *Type Locality*

South pit of the Atlanta Sand and Supply Company, Gaillard, Georgia, approximately 9.5 km southeast of Roberta in Crawford County (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W) (Herendeen et al. 1995).

#### *Stratigraphic Position*

Buffalo Creek Member, Gaillard Formation.

#### *Age*

Late Santonian (Late Cretaceous).

#### *Description and Remarks*

The new species is established for staminate flowers (figs. 1–17), bisexual flowers (figs. 18–23), fruits (figs. 24–38), and cupules (figs. 39–50). The floral organization of the staminate and bisexual flowers is summarized in figure 51.

**Staminate flower.** Staminate flowers are pedicellate and actinomorphic (figs. 1, 2, 5). The perianth consists of six free, imbricate tepals in two whorls of three (figs. 1, 4, 5). Tepals are ca. 0.9 mm long and ca. 0.25 mm wide at the base and taper to an acute apex, with numerous simple trichomes on the margins and abaxial surface (fig. 3).

The androecium is composed of 12 free stamens in two cycles of six (figs. 5–8). Between adjacent stamen bases is a slender, elongated, thin-walled structure (ca. 0.1 mm in diameter and ca. 0.4 mm long) that we interpret as a nectary lobe (figs. 5, 6, 8). Stamens consist of a filament and dorsifixed anther (figs. 9–12). Filaments are thin (ca. 0.1 mm in diameter), with simple trichomes (figs. 6, 9), and at maturity extend beyond the tips of the tepals (fig. 2). Mature stamens have distinctive, swollen filament bases (figs. 7–9). Anthers are ca. 0.2 mm long and dehisce by simple longitudinal slits (figs. 10–12). The anthers have a wrinkled epidermal surface but are more or less smooth internally (within the theca) (figs. 10, 11). The anthers are dorsifixed and the thecae are connected for approximately two-thirds the length of the anther (figs. 10, 12). The connective is developed into a distinctive, knoblike apical projection, ca. 0.4 mm wide at the base and ca. 0.4 mm long (fig. 11). The cycle of stamens opposite the tepals develops first, followed by the cycle alternate to the tepals, as evidenced by the relative maturity of anthers (figs. 7, 10, 12, 15) and the differing degree of enlargement of the filament bases (figs. 7, 8). In the bud, anthers of the cycle opposite the tepals are positioned above those of the alternate cycle

(figs. 7, 15). Pollen grains are tricolporate and small (polar axis ca. 12–13  $\mu\text{m}$  long, diameter ca. 9–11  $\mu\text{m}$ ), with a finely perforate tectum (fig. 13).

The flowers have a vestigial, tricarpellate gynoecium with three styles that are partially connate at the base. The ovary is absent. The free portion of each style is terete, tapering distally (fig. 14). A stigmatic surface is not apparent, but the majority of specimens are preserved with the gynoecium broken below the level at which the styles diverge. None of the specimens shows evidence of an ovary. There are simple trichomes in the center of the flower, around and between the style bases (fig. 14). Numerous small, multicellular, glandular structures (diameter ca. 0.6 mm) are scattered on the surface of the style bases (figs. 16, 17).

**Bisexual flower.** The bisexual flowers are epigynous and actinomorphic (figs. 18–21). The perianth, which is abraded in many specimens, is comprised of six free, imbricate tepals in two whorls of three (figs. 19–21, 46, 47). Tepals are ca. 0.9 mm long and ca. 0.25 mm wide at the base and taper to an acute apex (figs. 19, 46, 47).

The androecium consists of 12 free stamens in two cycles of six (figs. 20, 21). Between adjacent stamen bases is a slender, thin-walled structure (ca. 0.1 mm in diameter and ca. 0.4 mm long) that we interpret as a nectary lobe (figs. 21, 22). Stamens consist of thin filaments and dorsifixed anthers (figs. 20, 27–29). Filaments are thin (ca. 0.1 mm in diameter), with simple trichomes (figs. 20–22). Mature stamens have distinctive, swollen filament bases (figs. 23, 26). Anthers are ca. 0.2 mm long and dehisce by simple longitudinal slits. The anthers have a wrinkled epidermal surface pattern and are more or less smooth internally (within the theca) (figs. 27–29). Anthers are dorsifixed and the thecae are connected for approximately two-thirds the length of the anther (figs. 27, 28). The connective is developed into a distinctive, knoblike apical projection, ca. 0.4 mm wide at the base and ca. 0.4 mm long (fig. 27). Pollen grains are tricolporate and small (polar axis ca. 12–13  $\mu\text{m}$  long, diameter ca. 8–11  $\mu\text{m}$ ), with a finely perforate tectum (figs. 30–32).

The gynoecium is tricarpellate, with three styles that are partially connate at the base. The free portion of the styles is terete, tapering toward the tip (figs. 18, 21, 33, 34). A stigmatic surface is not apparent, but the majority of specimens are preserved with the gynoecium broken below the level at which the styles become free. There are numerous simple trichomes on the surface around and between the styles (figs. 21–23). Numerous small, multicellular, glandular structures (diameter ca. 0.6 mm) are scattered on the surface of the style bases (figs. 34, 35). The ovary is trilocular, with two anatropous, pendulous ovules per locule (figs. 36–38). There is no evidence of locular trichomes.

**Fruit.** Mature fruits are ca. 3.2 mm high (not including perianth, which is usually broken or abraded), with longitudinally ribbed fruit walls (three to five ribs

per side). The prominence of ribbing differs between specimens and is not correlated with the size and degree of maturity of the fruit/seed (based on ovule/seed development) (figs. 18, 19, 24, 25). In cross section, the fruits are triangular, with nearly equal sides (ca. 1–2 mm in width on each face) (figs. 20, 49). The perianth is comprised of six free tepals in two whorls of three but is abraded in most specimens (figs. 21, 24–26). Tepals of the outer whorl are located at the corners of the fruit and tepals of the inner whorl are centered on each face (figs. 20–26). Tepals taper to an acute apex. The apex of the fruit is pyramidal (figs. 18, 24). There are simple trichomes around and between the style bases (figs. 21–23). Numerous small, multicellular, glandular structures (diameter ca. 0.6 mm) are scattered on the surface of the style bases of the fruits (fig. 35). Immature fruits have a spongy mesocarp surrounding the locules and a central vascular bundle running from the base to apex of the fruit (fig. 37). Mature fruits contain a single seed, which fills the entire inner cavity of the fruit.

**Cupule.** Bisexual flowers and fruits are borne in cupules (figs. 39–50). Three cupule specimens, each containing fruits at different stages of maturity, have been recovered from the same samples that yielded the staminate flowers, isolated fruits, and isolated anthers. The degree of maturity of the cupules and fruits is inferred from their relative size and the developmental stage of the fruits.

Cupules of *Antiquacupula sulcata* are four-lobed and pedunculate. One cupule specimen (PP44751) contains six closely aggregated immature fruits, each subtended by multiple series of bracts (figs. 39–43). The cupule is 5.0 mm from base to apex, 2.0 mm in maximum width, and 3.5 mm in maximum breadth. Outermost in the cupule are four large bracts, each subtending one of the four primary lobes of the cupule (figs. 39, 40). Internal to this series is a second series of four large bracts with the same positioning (figs. 39, 40). Adaxial to each of these are one to two series of two smaller, narrower bracts. The most complete cupule specimen (figs. 39–43) contains at least six fruits, and the poorly preserved bases of additional fruits also may be present (fig. 41). In this specimen, the central immature fruit in the cupule is tetracarpellate, but details of the androecium and tepal structure are not clear (fig. 43). The remaining immature fruits in the cupule are tricarpellate, and of the numerous isolated fruits studied, none are tetracarpellate. One tricarpellate fruit is preserved with elongate filaments and intact and nearly mature anthers (fig. 42).

The second cupule specimen (PP44753) contains three tricarpellate fruits subtended by two series of bracts (figs. 44–47). The fruits are arranged in a row, with the central fruit raised slightly above the laterals. The cupule is 2.4 mm from base to apex. In the transverse plane, the cupule apex is 1.1 mm in maximum width and 2.6 mm in maximum breadth. The specimen is abraded at the base and it is possible that originally there were further series of bracts external to those

preserved. Outermost in the cupule is a series of four large bracts, each of which subtends one of the four primary lobes of the cupule (figs. 44, 45). Internal to each is a second series of two smaller, narrower bracts. The fruits contained within the cupule are all triangular, tricarpellate, and of approximately equal size. The fruits are identical in structure to those found isolated (figs. 33, 46, 47). One lateral fruit was preserved with an immature anther with the characteristic apical projection. Pollen grains are poorly preserved but tricolporate and 8–11  $\mu\text{m}$  in diameter. The sides of the cupule are slightly concave, flaring outward at the level of the fruit apices. In contrast, in the presumed more mature specimen (figs. 48–50), the cupule is more rounded at the base, suggesting that as the developing fruits enlarge, the cupule broadens at the base.

The third cupule (PP44752), interpreted as the most mature, is incomplete and consists of two cupule lobes subtending a single, mature tricarpellate fruit (figs. 48–50). This cupule is broken on one side. Each cupule lobe is composed of four series of bracts (fig. 50). The cupule is 2 mm from base to apex and at the apex is 2 mm along the broken edge and 1.5 mm wide from the center of the broken edge to outer bracts at the point of maximum diameter. The outermost structure in the cupule fragment is a single continuous bract (fig. 48). Internal to this is a series of two large bracts, each subtending a side of the fruit. Adaxial to each of these are two bracts, which in turn subtend a series of two smaller, narrower bracts (fig. 50). Numerous simple trichomes are present on the abaxial surfaces of the bracts. The shape and size of the fruit (ca. 1–2 mm long on each face) and the size of the cupule indicate that this is a relatively mature specimen. In addition, the shape of the cupule fragment is strongly convex and relatively wider at the base.

#### *Association of Fruits, Flowers, and Cupules*

We interpret the fossil staminate flowers (figs. 1–17), bisexual flowers and fruits (figs. 18–38), cupules (figs. 39–50), and isolated anthers (fig. 11) as parts of the same plant species for the following reasons: (i) staminate flowers have the same structural organization as the bisexual flowers and fruits, except for the presence of a vestigial rather than functional gynoecium (figs. 5, 20, 51); (ii) staminate flowers, isolated fruits, and fruits preserved within cupules show similar swollen filament bases at maturity (figs. 8, 23, 26); (iii) both staminate and bisexual flowers have comparable slender, thin-walled nectary lobes between the stamen bases (figs. 6, 22); (iv) both staminate and bisexual flowers have a distinctive apical projection on anthers (figs. 11, 27); (v) pollen identical to that produced by the staminate flowers occurs on the apical portions of eight fruit specimens and in high concentrations on a single fruit specimen preserved with intact filaments (figs. 13, 30–32); (vi) distinctive multicellular glandular structures are scattered on the surface of the gynoecium of the staminate flowers, bisexual flowers, and fruits (figs. 16, 17, 35); (vii) cupule specimens

have bisexual flowers/fruits preserved *in situ* that are morphologically identical to isolated fruits (figs. 20, 42, 49).

## Discussion

### Systematic Relationships of *Antiquacupula*

The quality of preservation of *Antiquacupula* and the availability of staminate flowers, bisexual flowers, fruits, cupules, and isolated anthers provide numerous characters for evaluating the systematic relationships of the reconstructed plant (table 1). Under traditional interpretations, the presence of a cupule, trimerous flowers, and an inferior, trilocular ovary with two apically attached, pendulous, anatropous ovules per locule are all characters of extant Fagaceae *sensu lato*. The presence of a cupule is widely considered the most diagnostic feature of Fagaceae *sensu lato*. Together these features support the relationship of *Antiquacupula* to the Fagaceae *sensu lato*. However, at a more detailed level, the data are insufficient for confident assignment to a particular taxon within Fagaceae *sensu lato*. *Antiquacupula* shares characters with both Nothofagaceae and Fagaceae *sensu stricto* (table 1), as well as with some families of Rosidae. In particular, *Antiquacupula* and Fagaceae *sensu stricto* both have dorsifixed anthers (vs. basifixed anthers in *Nothofagus*) and two cycles of tepals (vs. one cycle in *Nothofagus*). However, like *Nothofagus* and several species of *Quercus* (P. S. Manos, personal communication), *Antiquacupula* has a pronounced extension of the connective (lacking in most Fagaceae *sensu stricto*) and, as far as can be determined from the material available, also has glabrous fruit locules (Fagaceae *sensu stricto* have locular trichomes). *Antiquacupula* differs from both Fagaceae *sensu stricto* and Nothofagaceae in the possession of some likely plesiomorphic features such as well-developed nectary lobes and multicellular glands on the ovary surface (absent in extant Fagaceae but present in some rosids) and in the structure of the pollen tectum (perforate) (table 1).

Evaluating the relationships of *Antiquacupula* is further complicated by uncertainties in the relationships among extant Fagaceae. Recent cladistic analyses of morphological and/or molecular data have shown the Fagaceae *sensu lato* to be paraphyletic, and *Nothofagus* has been recognized as a separate family from Fagaceae *sensu stricto* (Nixon 1989; Chase et al. 1993; Manos et al. 1993; Manos 1997; Manos and Steele 1997). Under this interpretation, the presence of a cupule is no longer an unambiguous synapomorphy for the group (fig. 52), and thus the presence of a cupule in the fossil taxon supports a relationship to this fagaceous grade, but it does not help to resolve relationships with respect to Fagaceae *sensu stricto* versus Nothofagaceae. Therefore, the approach we take here is to assign *Antiquacupula* to Fagaceae *sensu lato*, with the recognition that future work may require that this assignment be revised as relationships among extant Fagaceae and Nothofagaceae become clearer.

**Table 1** Comparison of Morphological Features in Nothofagaceae, Fagaceae *sensu stricto* (Subfamilies Fagoideae and Castaneoideae), *Protofagaceae*, and *Antiquacupula*

Taxon	Num-ber of tepal cycles	Number of carpels	Fruit locules	Nectary lobes	Stami-nodes in pistillate flower	Fruit cross section	Number of stamens	Anther attachment	Pollen exine	Pollen size ( $\mu\text{m}$ )	Staminate flowers	Pistillode in staminate flower
Nothofagaceae ...	1	2 (central) 2 or 3 (lateral)	Glabrous	Absent	Absent	Lenticular and triangular	8-40	Basifixed	Psilate with microspinules	20 × 30	Pedicellate	Absent
Fagoideae .....	2	3	Trichomes	Absent	Absent	Triangular	6-16	Basifixed to dorsifixed	Scabrate, verrucate, rugulate	18 × 20 to 44 × 43	Pedicellate (Fagus) Sessile (other Fagaceae)	Absent
Castaneoideae ...	2	3-9	Trichomes	Absent	Present	Rounded irregular	(6-12)(-18)	Dorsifixed	Smooth anastomosing striate	15 × 9 to 20 × 15	Sessile	Sometimes present
<i>Protofagaceae</i> ...	2	2 (central) 3 (lateral)	Trichomes	Absent	?	Lenticular and triangular (one side broader than others)	(8-12)	Dorsifixed	Microfoveolate	6 × 4 to 8 × 6	Sessile	Three styles present, surrounded by trichomes
<i>Antiquacupula</i> ...	2	3	?Glabrous	Present	Bisexual	Triangular (equal length sides)	12	Dorsifixed	Finely perforate	10 × 15	Pedicellate	Three styles present, surrounded by trichomes

Note. The subfamily Fagoideae contains the genera *Fagus*, *Quercus*, *Trigonobalanus*, *Colombobalanus*, and *Formanodendron* (Nixon 1989). The subfamily Castaneoideae contains the genera *Chrysolepis*, *Castanea*, *Castanopsis*, and *Lithocarpus* (Nixon 1989).

<sup>a</sup> Specimens are not sufficiently well preserved to determine if stamens of pistillate flowers were fertile or staminal.

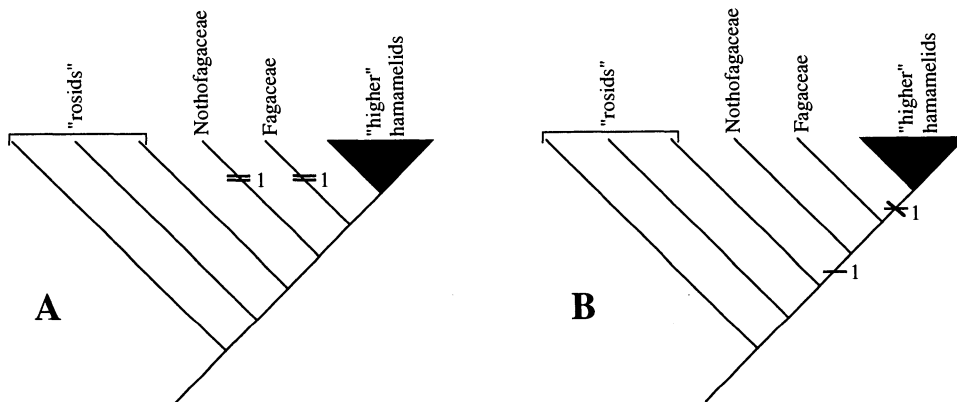
There has been considerable debate over the evolutionary origin of the fagaceous cupule (Berridge 1914; Hjelmqvist 1948; Brett 1964; Forman 1966b; Abbe 1974; Endress 1977; MacDonald 1979; Fey 1981; Fey and Endress 1983; Kaul and Abbe 1984; Nixon 1989; Jenkins 1993; Herendeen et al. 1995) and the question is further complicated by the possibility that the structure evolved twice, or evolved once and has been lost in a number of groups related to the Fagaceae (fig. 52). Nixon (1989) supported the interpretation of nonhomology among the cupules of Nothofagaceae and Fagaceae *sensu stricto* with observations that cupules in Fagaceae *sensu stricto* consistently have valves numbering one more than the total number of flowers ( $n + 1$ ), while the cupules of *Nothofagus* have more variation in the flower-to-valve ratio. However, recent work (Manos 1997) shows that the species of *Nothofagus* with cupules that deviate from the  $n + 1$  plan are derived within the genus.

The cupule of *Antiquacupula* (four-lobed and bearing at least six bisexual flowers, with the lateral flowers subtended by multiple [possibly four] series of bracts) appears to violate the  $n + 1$  rule. In contrast, *Protofagaceae*, with three pistillate flowers per four-lobed cupule, clearly conforms to the  $n + 1$  rule and thus is consistent in cupule structure with Fagaceae *sensu stricto*. Detailed morphological study of cupules in extant and extinct Fagaceae, coupled with clarification of relationships among extant hamamelids, selected lower rosids, *Protofagaceae*, and *Antiquacupula* will be crucial to further clarification of homologies of the fagaceous cupule and the evolutionary history of the Fagaceae.

#### Comparison of *Antiquacupula* and *Protofagaceae*

*Antiquacupula* shares several morphological features with *Protofagaceae*, which was described from the same fossil assemblage and was also assigned to the Fagaceae *sensu lato* (Herendeen et al. 1995) (table 1). The two taxa are similar in floral structure, with six tepals in two cycles of three, and 12 stamens in two cycles of six (typical of Fagaceae *sensu stricto*). In addition, both have dorsifixed anthers with thecae that are separated in the apical portion of the anther, tricolporate pollen, and unisexual staminate flowers. However, the flower, fruit, and cupule morphology of *Antiquacupula* and *Protofagaceae* differ in several significant features. The swollen stamen bases, the knoblike extension of the connective, multicellular glands on the gynoecium, and the presence of nectary lobes are all highly distinctive characteristics of *Antiquacupula* flowers that are absent in *Protofagaceae*. In addition, the two genera differ in pollen size and exine sculpture and in the shape of the fruits (*Antiquacupula* fruits have equal-width sides; *Protofagaceae* fruits have unequal-width sides).

The pedicellate staminate flowers of *Antiquacupula* differ from the sessile, staminate flowers of *Protofagaceae*, as well as from those of most extant Fagaceae *sensu lato*, which are all sessile except for *Fagus* and *Nothofagus* (Heywood 1993) (table 1). The pistillode is also relatively well developed in the staminate flowers of *Antiquacupula* (although the ovary itself is very



**Fig. 52** Cladograms illustrating two contrasting hypotheses of cupule evolution. Relationships of “rosids,” Nothofagaceae, Fagaceae, and “higher” hamamelids (e.g., Betulaceae, Myricaceae, and Juglandaceae) based on results from cladistic analysis of chloroplast DNA sequence data by Manos and Steele (1997). A, Hypothesis suggesting two independent origins of the cupule (1) in Nothofagaceae and Fagaceae. B, Hypothesis suggesting a single origin of the cupule and subsequent loss in the lineage leading to the “higher” hamamelids.

poorly developed), compared to the greatly reduced gynoecium of *Protofagaceae*. This is consistent with the interpretation that *Antiquacupula* retains more of the plesiomorphic characteristics of bisexual flowers and entomophily (e.g., nectary lobes) encountered in many rosoid taxa. The apparent absence of trichomes in the fruit locule of *Antiquacupula* (not unequivocally confirmed because of poor preservation) may be another significant difference from other members of the Fagaceae *sensu stricto* and *Protofagaceae*.

The cupules associated with *Protofagaceae* by Herendeen et al. (1995) closely resemble those containing fruits of *Antiquacupula* in overall shape and in being four-valved (cf. figs. 39–50 here with figs. 49–57 of Herendeen et al. [1995]). However, there are several key features in which these cupules differ. The cupules of *Antiquacupula* contain as many as six fruits, and all of the numerous isolated specimens are tricarpellate, as are all of the fruits preserved in cupules (except for one tetracarpellate central fruit in the immature six-fruited cupule). In contrast, mature cupules of *Protofagaceae* bear three abscission scars: two laterals that are triangular in shape and a central oblong scar that is thought to have been formed by a lenticular, bicarpellate fruit. Although none of the *Protofagaceae* cupules studied thus far is preserved with fruits *in situ*, both tricarpellate (triangular) and bicarpellate (lenticular) fruits of *Protofagaceae* have been recovered as isolated specimens, supporting the association made by Herendeen et al. (1995) on the basis of the size and shape of the scars.

#### Evolutionary Implications of *Antiquacupula*

The discovery of *Antiquacupula sulcata* from the same fossil assemblage that yielded *Protofagaceae alonensis* (Herendeen et al. 1995) establishes the divergence of at least two lineages of Fagaceae *sensu lato* by the Santonian (Late Cretaceous). Previously, the presence of castaneoid and trigonobalanoid (subfamily Fagoideae) infructescences and fruits from the Paleocene of Tennessee has been used to indicate the divergence of the two subfamilies of Fagaceae (castaneoids

and fagoids) by the early Tertiary or Late Cretaceous (Crepet and Nixon 1989a). The discovery of *Antiquacupula* provides evidence of a Cretaceous diversity in the family and supports the dispersed pollen record in documenting the presence of Fagaceae *sensu lato* by at least the Campanian (*Nothofagus*-like pollen reported by Dettman et al. 1990). Current phylogenetic hypotheses indicate that the Fagaceae are nested within the largely insect-pollinated rosids (fig. 52) but, because they are also closely related to several predominantly wind-pollinated groups of extant “higher” hamamelids, the family can be thought of as somewhat intermediate in a trend from entomophilous plants with tricolporate pollen to anemophilous plants with triporate and stephanoporate pollen (Nixon 1989). *Antiquacupula* and *Protofagaceae* contribute new data on some of the early Fagaceae that may have been involved in this transition. The presence of nectary lobes in *Antiquacupula* is an especially interesting feature that, as far as we know, does not occur in any extant Fagaceae. As further information accumulates on early Fagaceae, comparisons with fossil flowers of the Normapolles complex, as well as with extant and fossil rosids, should be important in clarifying patterns of morphological evolution in this important group of flowering plants.

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## Literature Cited

- Abbe EC 1974 Flowers and inflorescences of the "Amentiferae." Bot Rev 40:159–261.
- Berridge EM 1914 The structure of the flower of Fagaceae, and its bearing on the affinities of the group. Ann Bot 28:509–526.
- Brett DW 1964 The inflorescence of *Fagus* and *Castanea*, and the evolution of the cupules of the Fagaceae. New Phytol 63:96–118.
- Chase MW, DE Soltis, RG Olmstead, D Morgan, DH Les, BD Mishler, MR Duvall, et al 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. Ann Mo Bot Gard 80:528–580.
- Chmura CA 1973 Upper Cretaceous (Campanian-Maastrichtian) angiosperm pollen from the western San Joaquin valley, California, U.S.A. Palaeontographica Abt B 141:89–171.
- Christopher RA 1979 Normapollens and triporate pollen assemblages from the Raritan and Magothy Formations (Upper Cretaceous) of New Jersey. Palynology 3:73–122.
- Crane PR, PS Herendeen 1996 Cretaceous floras containing angiosperm flowers and fruits from eastern North America. Rev Palaeobot Palynol 90:321–340.
- Crepet WL 1989 History and implications of the early North American fossil record of Fagaceae. Pages 45–66 in PR Crane, S Blackmore, eds. Evolution, systematics and fossil history of the Hamamelidae. Vol 2. "Higher" Hamamelidae. Oxford University Press, Oxford.
- Crepet WL, CP Daghljan 1980 Castaneoid inflorescences from the middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. Am J Bot 67:739–757.
- Crepet WL, KC Nixon 1989a Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. Am J Bot 76:842–855.
- 1989b Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. Am J Bot 76:1493–1505.
- Daghljan CP, WL Crepet 1983 Oak catkins, leaves and fruits from the Oligocene Catahoula Formation and their evolutionary significance. Am J Bot 70:639–649.
- Dettmann ME, DT Pocknall, EJ Romero, J Del, C Zamalao 1990 *Nothofagidites* Erdtman ex Potonié 1960: a catalogue of species with notes on the palaeogeographic distribution of *Nothofagus* Bl. (Southern Beech). NZ Geol Surv Paleontol Bull 60. 79 pp.
- Endress PK 1977 Evolutionary trends in the Hamamelidales-Fagales group. Plant Syst Evol Suppl 1:321–347.
- Fey BS 1981 Untersuchungen über Bau und Ontogenese der Cupula, Infloreszenzen und Blüten sowie zur Embryologie bei Vertretern der Fagaceae und ihre Bedeutung für die Systematik. PhD Diss. University of Zurich. 185 pp.
- Fey BS, PK Endress 1983 Development and morphological interpretation of the cupule in Fagaceae. Flora 173:451–468.
- Forman LL 1964 *Trigonobalanus*, a new genus of Fagaceae, with notes on the classification of the family. Kew Bull 17:381–396.
- 1966a Generic delimitation in the Castaneoideae (Fagaceae). Kew Bull 18:421–426.
- 1966b On the evolution of cupules in the Fagaceae. Kew Bull 18:385–420.
- Herendeen PS, PR Crane, AN Drinnan 1995 Fagaceous flowers, fruits, and cupules from the Campanian (Late Cretaceous) of central Georgia, USA. Int J Plant Sci 156:93–116.
- Heywood VH 1993 Flowering plants of the world. Oxford University Press, New York.
- Hjelmqvist H 1948 Studies on the floral morphology and phylogeny of the Amentiferae. Bot Not 2(suppl):1–171.
- Huddleston PF, JH Hetrick 1991 The stratigraphic framework of the Fort Valley Plateau and the Central Georgia Kaolin District. Georgia Geological Society Guidebooks 11(1). Georgia Geological Society, Atlanta.
- Hutchinson J 1967 The genera of flowering plants. Vol 2. Dicotyledons. Oxford University Press, London.
- Jenkins R 1993 The origin of the fagaceous cupule. Bot Rev 59:81–111.
- Jones JH 1986 Evolution of the Fagaceae: the implications of foliar features. Ann Mo Bot Gard 73:228–275.
- Jones JH, DL Dilcher 1988 A study of the "*Dryophyllum*" leaf forms from the Paleogene of southeastern North America. Palaeontographica Abt B 208:53–80.
- Kaul RB, EC Abbe 1984 Inflorescence architecture and evolution in the Fagaceae. J Arnold Arbor Harv Univ 65:375–401.
- Keller JA, PS Herendeen, PR Crane 1996 Fossil flowers and fruits of the Actinidiaceae from the Campanian (Late Cretaceous) of Georgia. Am J Bot 83:528–541.
- Konopka AS, PS Herendeen, PR Crane In Press Sporophytes and gametophytes of Dicranaceae from the Campanian (Late Cretaceous) of Georgia, U.S.A. Am J Bot.
- Konopka, AS, PS Herendeen, GL Smith Merrill, PR Crane 1997 Sporophytes and gametophytes of Polytrichaceae from the Campanian (Late Cretaceous) of Georgia, U.S.A. Int J Plant Sci 158:489–499.
- Linder HP, MD Crisp 1995 *Nothofagus* and Pacific biogeography. Cladistics 11:5–32.
- MacDonald AD 1979 Inception of the cupule of *Quercus macrocarpa* and *Fagus grandifolia*. Can J Bot 57:1777–1782.
- Magallón-Puebla S, PS Herendeen, PK Endress 1996 Floral remains of the tribe Hamamelideae (Hamamelidaceae) from Campanian strata of southeastern U.S.A. Plant Syst Evol 202:177–198.
- Manchester SR 1981 Fossil plants of the Eocene Clarno Nut Beds. Oreg Geol 43:75–81.
- 1994 Fruits and seeds of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. Palaeontogr Am 58:1–205.
- Manos PS 1997 Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequences (ITS): taxonomic congruence with morphology and plastid sequences. Am J Bot 84:1137–1155.
- Manos PS, KC Nixon, JJ Doyle 1993 Cladistic analysis of restriction site variation within the chloroplast DNA inverted repeat region of selected Hamamelididae. Syst Bot 18:551–562.
- Manos PS, KP Steele 1997 Phylogenetic analysis of "higher" Hamamelididae based on plastid sequence data. Am J Bot 84:1407–1419.
- Martin PG, JM Dowd 1993 Using sequences of *rbcL* to study phylogeny and biogeography of *Nothofagus* species. Aust Syst Bot 6:441–447.
- Nixon KC 1989 Origins of Fagaceae. Pages 23–43 in PR Crane, S Blackmore, eds. Evolution, systematics and fossil history of the Hamamelidae. Vol 2. "Higher" Hamamelidae. Oxford University Press, Oxford.

## Note Added in Proof

The age of the Allon deposit was recently reinterpreted as late Santonian based on palynological evidence (R. A. Christopher, Clemson University, written communication, 1998). Although a palynologic zonation for the Upper Cretaceous of the southeastern Coastal Plain Province has yet to be published, Christopher examined terrestrial palynomorphs from the Allon locality and considers the sediments to be biostratigraphically equivalent with marine units that have been assigned a late Santonian age on the basis of calcareous nanofossils (i.e., equivalent to the lower part of calcareous nanofossil zone CC17, which Burnett [1996] considers late Santonian). The age of the Allon locality was previously cited as early Campanian based on a less precise understanding of the biostratigraphy (Herendeen et al. 1995; Crane and Herendeen 1996; Keller et al. 1996; Magallón-Puebla et al. 1996; Konopka et al. 1997).

Burnett JA 1996 Nanofossils and Upper Cretaceous (sub-)stage boundaries—state of the art. J Nannoplankton Res 18:23–32.